ESTIMATING PREDATION IMPACT ON HONEYBEES *APIS MELLIFERA* L. BY EUROPEAN BEE-EATERS *MEROPS APIASTER* L.

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RÉSUMÉ

Nous avons étudié la pression de prédation sur les abeilles (*Apis mellifera* L.) par les Guêpiers d'Europe dans cinq zones de l'île de Sardaigne (Italie centrale). Le nombre des colonies d'oiseaux augmentait avec celui des sources de nourriture (ruches et ruchers) ; par contre, ni le nombre total d'oiseaux ni la taille des colonies n'étaient liés au nombre de ruches. Les guêpiers ont prélevé les ouvrières en fonction de leur disponibilité totale moyenne (calculée sur toutes les zones d'étude), mais la prédation sur les abeilles s'est également produite là où les ruches étaient absentes ou très éloignées. En revanche, la prédation sur les faux-bourdons était négativement corrélée avec leur disponibilité totale moyenne. Pourtant, la prédation sur les abeilles était liée négativement à celle sur les faux-bourdons.

La pression de prédation sur les ouvrières était en moyenne de 0,37 % (intervalle : 0,26-0,58 %) de leur disponibilité totale moyenne de mai à juillet. La mortalité quotidienne des abeilles par ruche due à la prédation par les guêpiers était en moyenne de 6,1 % (n = 73) de leur mortalité quotidienne totale. La pression de prédation sur les faux-bourdons était en moyenne de 0,91 % (intervalle : 0,27-1,43 %) de leur disponibilité totale moyenne de mai à juillet. La mortalité quotidienne des faux-bourdons par ruche due à la prédation par les guêpiers représentait en moyenne 30 % (n = 4) de leur mortalité quotidienne totale. L'impact de la prédation sur les abeilles était indépendent de la densité de proies, tandis que celui sur les faux-bourdons était négativement lié à la densité des proies et donc dilué aux densités élevées de ruches. L'impact économique sur l'apiculture par les Guêpiers d'Europe est considéré comme négligeable mais les pertes de faux-bourdons ont été localement importantes et potentiellement préjudiciables à des apicultures de petite taille ou spécialisées.

SUMMARY

We studied predation pressure on honeybees (*Apis mellifera* L.) by European bee-eaters (*Merops apiaster* L.) in five areas with varying bird and insect populations, on the island of Sardinia (Italy). Number of bee-eater colonies increased with number of food sources (hives and apiaries); conversely total bird population and colony size were not related to food sources. Bee-eaters preyed on bees (foragers) in relation to their mean total availability (calculated over all study areas), but predation on bees occurred also where hives were absent or far away. By contrast, predation on drones was negatively correlated to their mean total availability. Indeed, predation on foragers and drones correlated negatively.

Predation impact on foragers was on average 0.37 % (range: 0.26-0.58 %) of their mean total availability during May-July. The daily forager mortality per hive due to bee-eater

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predation represented on average 6.1 % (n = 73) of their total daily mortality per hive. Predation pressure on drones was on average 0.91 % (range: 0.27-1.43 %) of their mean total availability during May-July. The daily drone mortality per hive due to bee-eater predation represented on average 30 % (n = 4) of their total daily mortality per hive.

Predation impact by bee-eaters on foragers was independent from prey density. Conversely, predation on drones was inversely dependent from prey density, thus it was diluted at high hive densities. The economic impact on apiculture by bee-eaters was in general negligible, but losses of drones were locally important and potentially detrimental to small or specialized apicultures.

INTRODUCTION

The European bee-eater *Merops apiaster* L. is a summer visitor to the Mediterranean region where it breeds colonially in nest-holes, usually dug in sloping earth, steep sand banks or in level ground. Its food consists almost exclusively of flying insects caught on the wing (Fry, 1984; Krebs & Avery, 1985). Hunting is generally well within 1 to max. 3 km of the nest, but parents will sometimes forage up to 12 km away (Tostain, 1978). Studies of the food of *M. apiaster* carried out in a number of European countries (most cited in Fry, 1984) showed that Hymenoptera always predominated in diet samples, with proportions varying from 51 % to 91 %.

Western honeybees *Apis mellifera* L. form on average about one-third of the Hymenoptera preyed on by bee-eaters and appear to be caught selectively (Petrov, 1954; Helbig, 1982; Inglisa *et al.*, 1993; Grenci *et al.*, 1997) since in nature they seldom constitute the majority of flying insects, except near their hives. Moreover, the distributional range of *Apis* is congruent with that of the family Meropidae which suggests that bee-eaters have evolved as predators of honeybees (Fry, 1984). Honeybees are profitable prey because of their short pursuit and handling time and the stable and predictably high rate of encounters in certain patches (Krebs & Avery, 1985). Furthermore, their quality (nutrient content) is high (Cavani, 1991). Also, drone honeybees appear to be preferred to workers (Matousek, 1951; Ursprung, 1979; Fry, 1984).

Clearly, the preference for domestic bees may cause damage to apiaries: for example, a single bee-eater has been estimated to account for 9 000 honeybees during its summer stay in the Ukraine (Petrov, 1954). In South-Africa, European bee-eaters were "rather a serious nuisance" (Buys, 1975) and were considered as pests of apiculture in Hungary (Szederkényi *et al.*, 1956), the former USSR (Yakubanis & Litvak, 1962) and Algeria (Jenn, 1973).

In Italy, and particularly in Sardinia, the public administration had paid hundreds of millions of liras (150 000 ECU) in recent decades to bee-keepers complaining of serious damage, including the loss of queens, to their apiaries by bee-eaters. The simple presence of bee-eaters near apiaries is often enough to convince bee-keepers that they are a nuisance. Unfortunately, although the bee-eater is nominally protected by law in most Mediterranean countries, including Italy, many birds are shot each year by irate bee-keepers. This is probably by far the most frequently used "control" measure worldwide (Woldheck, 1979).

In fact, however, no detailed quantitative study based on bee availability has been carried out to estimate the importance of bee predation by bee-eaters. The most extensive investigation of their pest status ever undertaken was in Kazakh-

stan, in 1936 (Korelov, 1948): 500 European bee-eaters were shot in order to evaluate their diet and it was concluded that they were, on balance, economically valuable since the birds also consumed many predators of honeybees (*e.g.* Hornets, *Vespa crabro*). Fry (1983 and references therein), after examining a total of 47,000 prey items in the diets of 17 *Merops* species in 25 countries, found that bee-eaters consumed one predator of honey bees every four honeybees.

Bee-eaters tend to raid apiaries in dull, cool weather (Fry, 1984), a relatively rare event during Mediterranean summers. Moreover, the insects themselves take effective action against bee-eater attacks, by reducing movement (Korelov, 1948) or by directly attacking birds (pers. obs.). Thus, the actual impact of bee-eaters on honeybees is controversial.

The aims of this work were to ascertain (i) relationships between bee and bee-eater populations, ii) predation rates on honeybees (both foragers and drones) by bee-eaters, (iii) predation impacts on honeybees (number of foragers and drones removed from the population by bee-eaters), and (iv) to suggest management guidelines to minimize or eliminate damage.

STUDY AREAS AND METHODS

The study was carried out on the island of Sardinia (Italy) in the periods May-July 1992 and 1995. We considered four sites where honeybees and bee-eaters were both present; a fifth site, Riola, where neither domestic nor wild hives were present, was chosen as a control area. Two sites were in the west part of the island: Arborea and Riola (Oristano Province), and the others were in the southeast part (Fig. 1): Muravera, Corongiu and Torre Salina (Cagliari Province). Apiculture was intensive-professional at Muravera and Torre Salina, semi-intensive at Arborea and non-professional at Corongiu. Losses of honey harvest varying from 35 to 100 % due to bee-eaters were cited by bee-keepers of Arborea, Muravera and Torre Salina.

A typical Mediterranean climate marks all these sites: the summer mean temperature is 25 °C (range 16-33 °C), with scarce and irregular rainfall, which may reach 30 mm monthly.

DATA COLLECTION

In each site except Riola, we selected a sampling area using a circle of 3 km radius centered on the largest apiary (number of hives) of the locality. The 3-km radius corresponds either to the maximum distance travelled from hive by foraging honey bees (Brian, 1965; Grout, 1981) and to the maximum extension of bee-eater foraging range through the breeding season (Swift, 1959; Fry, 1984). Within this area, we censused all bee-eater colonies by recording the total number of active nests, and measured the availability of honey bees by censusing all apiaries and bee-hives. Population size of bee hives (workers) grows exponentially from early March and peaks in May, remaining stable until late July and then declining almost linearly to a minimum in December (Brian, 1965; Grout, 1981). Drones appear in the hive only from April and their number peaks soon before nuptial flights in May-June; thereafter they decline, disappearing from hives in August (Prof. R. Hoopingarner, pers. comm.). During the flower season, mortality and recruitment

Figure 1. — Location of the study sites on the island of Sardinia. Boundaries of the Oristano and Cagliari Provinces are also reported.

were balanced (3 % of the total bee population in a hive, Lundie in Bodenheimer, 1958; Brian, 1965; R. Cirone and other bee-keepers, pers. comm.). We therefore assumed that, during the study period, each hive contained a stable mean of 40,000 workers (Dietz, 1982), only half of which (20,000 foragers) were actually available to bee-eaters. In addition, we assumed that drones (males) represented on average 1 % (Ruttner, 1966) of the total worker population in each hive (*i.e.* 400 drones). From these estimates, we calculated the daily recruitment/mortality rates for workers and drones (*i.e.,* 1,200 workers and 12 drones a day, respectively).

Habitats within each given sampling area were as follows: Muravera: 30 % orchards, 30 % meadows, 20 % dry crops (cereals), 10 % ricefields, 10 % uncultivated fields. Corongiu: 75 % dry crops (cereals, olive groves, vineyards), 25 % pastures-meadows. Torre Salina: 60 % pastures, 30 % uncultivated fields, 10 % dry crops (cereals). Arborea: 100 % dry crops. (cereals, vegetables). Riola: 100 % pastures-meadows.

After removing old pellets, all the pellets newly produced by *M. apiaster* adults in all bee-eater colonies within each sampling area were collected at fortnightly intervals starting from 15 May and finishing 31 July. Twenty pellets per sampling area were randomly selected from each fortnightly sample and were dissected in water. Thus the total sample we considered was 600 pellets. Prey were identified by binocular microscope to species, genus or family level using standard techniques (Vigna Taglianti *et al.*, 1988) and scored accurately by numbering

heads and wings. Bees were easily recognizable as they were swallowed whole immediately after capture or devenoming treatment, and heads and wings were not detached during this treatment (pers. observ.). Prey were then pooled into two categories: honeybees and all other prey. Thanks to different head and wing morphology, honeybees were further separated into workers and drones.

For each sampling area we calculated the monthly frequency (%) of bees/drones in bee-eater diets over the total prey. Then, for each fortnightly sampling unit (M1: 15 May, M2: 31 May, G1: 15 June, G2: 30 June, L1: 15 July, L2: 31 July), we averaged data coming from all sampling areas in order to calculate the following gross means: 1) predation rate as the mean number of foragers/drones per pellet collected during each sampling; 2) individual predation rate as the number of foragers/drones consumed per day by a bird, assuming the mean daily number of pellets produced by an adult bee-eater to be 5 (range 3.75-10, Ursprung, 1979; Fry, 1984); 3) total predation rate as the number of foragers/drones consumed per day by the mean number of birds present during each sampling, assuming two birds and an average of 0.2 helpers per nest (Cano, 1960; Fry, 1984). For bird calculation, we also took into account the chick presence adding 4 young per nest (Korodi & Libus, 1968; Lessels & Avery, 1989) to the number of birds in July. We assumed that chicks consumed up to 20 % more foragers/drones than adults (Ursprung, 1979), but they regurgitated only two pellets per day (Koenig, 1969).

Statistical analyses

Data not normally distributed were $\log_n$-transformed. We performed one-way ANOVA to test for differences in the mean bee predation rate (bees/pellet) between western and southeastern colonies of *M. apiaster*. We used simple Pearson correlation coefficients to analyse bivariate relationships between (i) the mean bee and bee-eater populations of each sampling area ($n = 5$), and (ii) the mean predation rates (bees and drones per pellet) and the mean availabilities of bees (number of hives) calculated over all sampling areas ($n = 5$) for each fortnightly sampling ($n = 6$). The same test was performed to study relationships between the mean predation impact by birds (*i.e.*, the percentage of bees and drones removed over the mean available bee population during each sampling) and the mean availability of bees calculated as above (number of hives). Chi-square tests on contingency tables were performed to compare the mean use of foragers and drones by bee-eaters of the sampling areas in which were present hives, with the mean bee availability during each fortnightly sampling.

RESULTS

Bee-eater and bee populations

Bird colonies in the study areas varied from 2 (Riola) to 11 (Muravera). Colony sizes varied from 100 nests/colony (Riola) to 7 nests/colony (T. Salina) being on average ($\pm$ S.E.) 33.2 ± 17.1 nests/colony. Therefore, Muravera area hosted the greatest bee-eater population whereas T. Salina supported the smallest and most diluted one (Table I).

TABLE I

Bee-eaters and bee populations in the study areas.

	MURAVERA W			CORONGIU W			T. SALINA W			ARBOREA E			RIOLA E		
	May	June	July	May	June	July	May	June	July	May	June	July	May	June	July
Colonies	11	11	11	4	4	4	5	5	5	8	8	8	2	2	2
Nests	328	328	328	51	51	51	35	35	35	132	132	132	200	200	200
Birds	722	722	2 034	112	112	316	77	77	217	290	290	818	440	440	1 240
Apiaries	17	15	14	1	1	1	3	3	3	4	4	7	0	0	0
Hives	795	521	537	36	31	31	117	117	133	97	97	277	0	0	0
Apiary size (hives/apiary)	47	35	38	36	31	31	39	39	44	24	24	40			
bee daily availability X1000	15 900	10 420	10 740	720	620	620	2 340	2 340	2 660	1 940	1 940	5 540	0	0	0

W: western areas; E: eastern areas.

Bee availability fluctuated in all sampling areas during the bee-eater breeding season due to the movement of hives (Table I) and varied from 795 hives (Muravera, first half of May) grouped in 17 apiaries to 0 (Riola). The mean number of apiaries per area was 6.1 ± S.E. 1.7 (range 1-17), while the mean number of hives per apiary was 36 ± S.E. 2.1 (range 24-47). Thus, bee population in each area was concentrated in few apiaries of medium-low size (50-100 hives per apiary are considered respectively the optimum and the maximum size in order to economically sustain bee-keeping, Grout, 1981).

The number of bee-eater colonies was positively correlated with both number of hives ($r_p = 0.91$, $p = 0.03$, $n = 5$) and apiaries ($r_p = 0.95$, $p = 0.01$, $n = 5$) in each study area (Fig. 2). On the other hand, the number of birds and the colony size (*i.e.* nests/colony) were not significantly related to bee availability in each study area (hives and apiaries, all p-values > 0.15, Pearson correlation test). Thus, the number of food sources favoured in some way bird dispersion in many medium-small colonies through the study areas.

BEE-EATER DIET

From 600 pellets we obtained 15,143 identifiable prey items, 4,802 of which were honeybees, for an overall frequency in diet of 31.7 % (8 bees per pellet on average, range 0-47). Remaining prey were mainly beetles (35 %), other Hymenoptera (25 %), butterflies, cicadas, crickets and Odonata (8 % all together). Drones were only 3.1 % (n = 148) of bees preyed upon.

The mean monthly percentage of foraging bees in bee-eater diets varied from 52.5 % (Muravera, range 46.2-62.5 %) to 10 % (Riola, range 3.9-19.9 %; Fig. 3). The mean monthly percentage of drones in the diets of bee-eaters was low and varied from 2 % (Corongiu, range 0-5.1 %) to 0.4 % (Riola, range 0-1 %; Fig. 3). Nonetheless, at Corongiu the frequency of drones in bee-eater diet reached the 23 % of foraging honey bees preyed on by bee-eaters in June (5.1 % of drones *vs* 22.3 % of foragers). In July, drones disappeared from bee-eater diets at all sites but

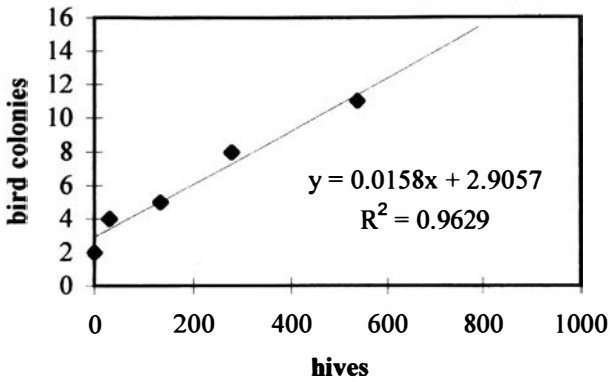

Figure 2. — Relationships between the mean number of bee-eater colonies and the mean bee availabilities (number of hives) in each study area.

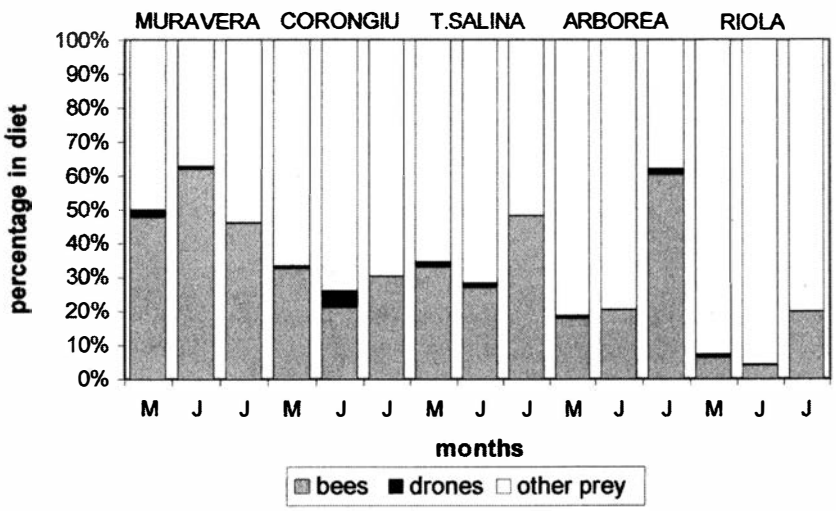

Figure 3. — Percentage of foraging bees, drones and other prey in the monthly diets of bee-eaters of each study area.

Arborea. At this site drones were absent from the June diet but were again consumed in July, just when 180 nomadic hives were set up in this area (Table I).

PREDATION RATES (FUNCTIONAL RESPONSE)

The mean number of bees per pellet (Table II) varied significantly between eastern and western bee-eater colonies, being 8.8 bees/pellet (± 7.4 SD, n = 240)

in eastern areas where the overall honeybee availability was greater, but 5.6 (± 7.6 SD, n = 360) in western areas ($F_{1,598} = 23.87$, p = 0.0000). In fact, the mean predation rates (functional response) on foraging bees by bee-eaters of all sampling areas closely followed variations of the mean hive availability during the whole sampling period ($r_p = 0.87$, p = 0.021, n = 6), and the mean hive availability explained 77 % of variation in the mean predation rate on foraging bees (Fig. 4). Thus, bee-eaters behaved partly opportunistically, preying on foraging bees in relation to their availability. However, data from Riola indicated that bee-eaters preyed on bees even when hives were absent or far-away from bee-eater nests, and this indicated selectivity on the part of bee-eaters for bees.

TABLE II

Mean predation rates on bees by bee-eaters during months and the whole sampling period.

Sampling Areas		bees/pellet			
		May	**June**	**July**	**Total**
Muravera	East	12.0	12.1	10.1	11.5
Corongiu	East	8.2	5.3	6.5	7.2
T. Salina	East	8.3	5.5	10.3	7.5
Arborea	West	3.3	4.5	12.8	6.8
Riola	West	1.4	0.8	7.5	3.0

$F_{4,594} = 17.1$, p = 0.000

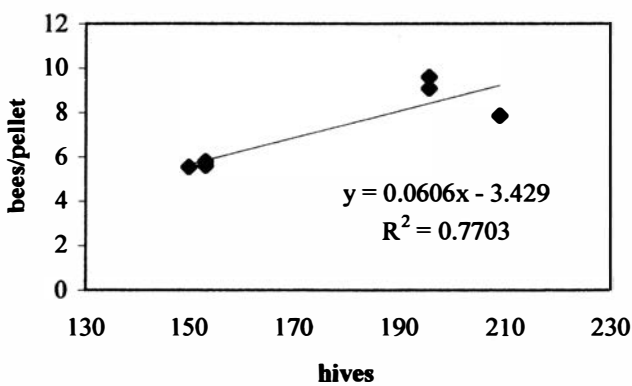

Figure 4. — Relationships between the mean hive availability and the mean predation rate on foragers through the sampling period. Regression line is also shown. Data from all sampling areas cumulated for each sampling.

In contrast, the mean drone predation rate varied negatively with the mean hive number throughout the sampling period ($r_p = -0.81$, p = 0.05, n = 6). This indicated that predation on drones can be very heavy at low bee-availabilities, but

rapidly decreases at higher prey densities (Fig. 5). Clearly, mean predation rates on foragers and drones were also inversely related ($r_p = -0.91$, $p = 0.013$, $n = 6$, Fig. 6).

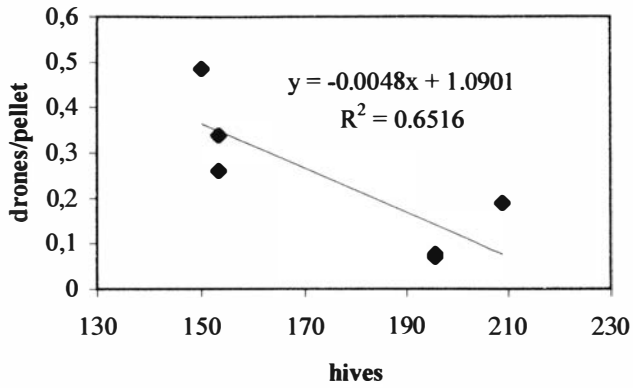

Figure 5. — Relationships between the mean hive availability and the mean predation rate on drones through the sampling period. Regression line is also shown. Data from all sampling areas cumulated for each sampling.

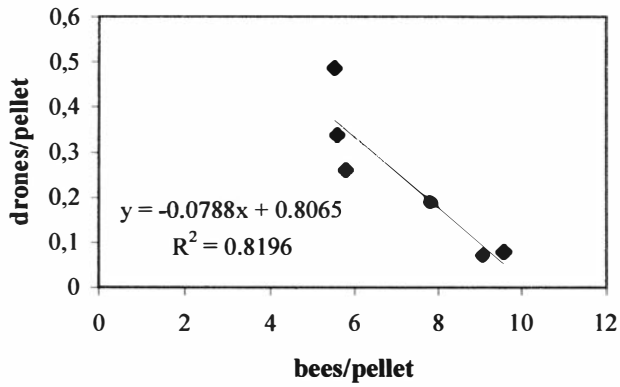

Figure 6. — Relationships between the mean predation rates on foragers and drones through the sampling period. Regression line is also shown.

PREDATION IMPACT ON BEES AND DRONES

The total mean predation rate, *i.e.* foragers removed daily over all sampling areas by the total mean of bee-eaters varied from *c.* 10,000 to *c.* 28,400 depending on sampling unit, being on average 16,650 foraging bees removed per day over the whole sampling period (Table III). Predation pressure throughout the sampling period was calculated averaging data from only four sampling areas; data from

Riola was excluded since there were neither domestic nor wild hives in a radius of 3 km around the larger of the bee-eater colonies located there. For each sampling unit we calculated the total mean predation pressure as the proportion (%) of foragers and drones removed daily from the mean bee population available by the mean number of bee-eaters. Since the population of bees and drones in a hive was considered stable through the month (see Data Collection), the daily predation pressure coincided with the monthly predation pressure.

TABLE III

Individual and total daily predation rate on foraging bees (five sampling areas) and mean total predation pressure on foraging bees (four sampling areas) in each sampling period (M1, M2; G1, etc.).

	M1	M2	G1	G2	L1	L2
Individual predation rate (n°)	46	34	35	35	70	75
Total predation rate (n°)	13,830	10,150	10,380	10,365	26,800	28,360
Total predation pressure (%)	0.265	0.271	0.271	0.271	0.548	0.58

The total mean predation pressure on foraging bees was constant during May-June (0.27 %), but duplicated in July (0.55-0.58 %), when bee-eaters were feeding chicks. (Table III). In fact, bee-eaters may have removed on average 0.37 % of the total mean bee availability over the whole three-month period, a very low percentage. In some areas (*e.g.* Muravera) bee-eaters may have consumed nearly 4.8 million foragers during their breeding season, that is the negligible 0.42 % of the local bee availability, whereas in others (Torre Salinas and Corongiu) bee-eaters caught less than half a million workers in three months (0.17 % and 0.73 % of the local bee availabilities respectively). Predation pressure on foraging bees was not density dependent ($r_p = 0.55$, $p = 0.26$, $n = 6$, Fig. 7), since it was constant during May-June and increased in July simply due to increased number of consumers (adults + chicks) at that time.

By contrast, daily predation impact on drones was in general stronger than predation impact on foraging bees throughout the sampling period, except in the first half of May, and peaked in July (Table IV). Thus the mean proportion of drones removed over the whole breeding season was 0.91 % of the total mean drone population, but reached 2.9 % of the local drone population in some areas (Corongiu). However, predation pressure on drones varied inversely to hive availability through the sampling period, so that predation on drones was diluted at high prey densities ($r_p = -0.97$, $p = 0.001$, $n = 6$, Fig. 8). In fact, bee-eaters strongly preferred drones over bees since the former were preyed on significantly more than they were available during all sampling units, but one (Fig. 9). However, drones completely disappeared from bee-eater diets in early summer. A sudden shift in food preference by bee-eaters during the peak of chick-rearing was

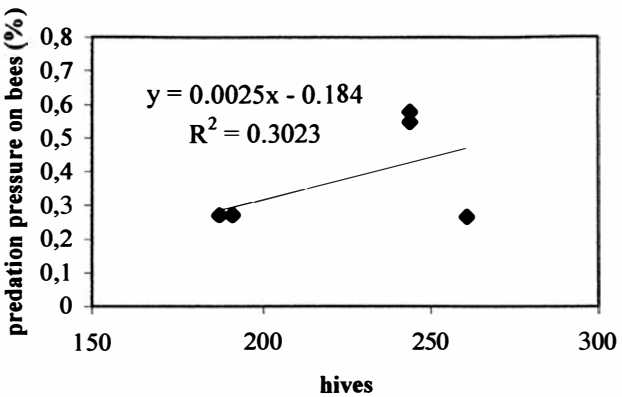

Figure 7. — Relationships between the mean predation pressure (%) on foragers and the mean hive availability through the sampling period. Regression line is also shown.

unlikely, considering the energetic value of drones (230 mg *vs* 95 mg of workers). Another explanation was that drones were given to chicks entirely, thus lacking from pellets of adult birds. However, the different trend of drone consumption by bee-eaters at Arborea study area (*i.e.* drones disappeared from adult pellet in June when adults were incubating and reappeared in July when adults were feeding young), seemed to rule out this hypothesis. Therefore, we believe that drones became nearly extinct in early summer due to starvation following their expulsion from hives. Nonetheless, predation by bee-eaters might have been at least partly responsible for drone extinction in some of the study areas (*e.g.*, Corongiu, see below).

TABLE IV

Individual and total daily predation rate on drones (five sampling areas) and mean total predation pressure on drones (four sampling areas) in each sampling period (M1, M2; G1, etc.).

	M1	M2	G1	G2	L1	L2
Individual predation rate (n°)	0.9	2.8	2.1	1.6	2.6	2.8
Total predation rate (n°)	284	912	623	471	951	1 031
Total predation pressure (%)	0.27	1.21	0.7	0.53	1.32	1.43

The hive predation pressure was calculated for each sampling unit as the mean number of foragers and drones removed daily per hive from the mean

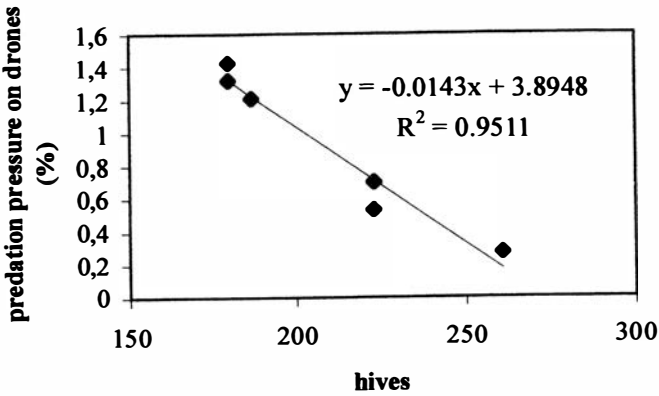

Figure 8. — Relationships between the mean predation pressure (%) on drones and the mean hive availability through the sampling period. Regression line is also shown.

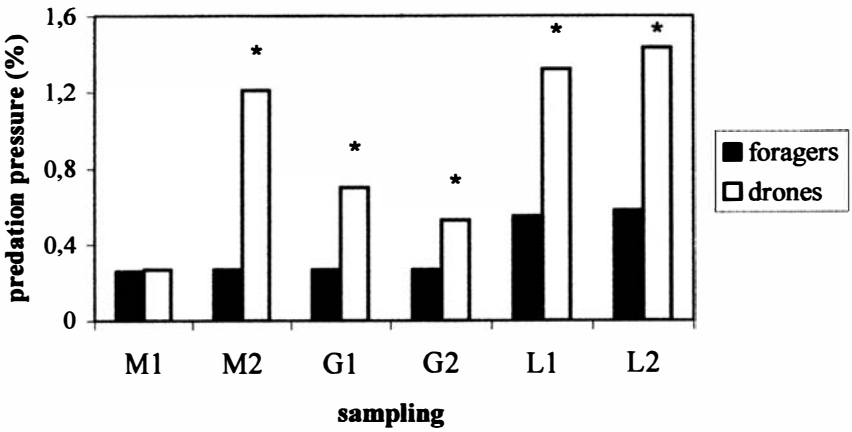

Figure 9. — Comparison between the mean predation pressure on foragers and drones through the sampling period. Asterisks indicate significant differences at P = 0.00000.

number of available hives by the mean number of bee-eaters, assuming that bee-eater predation was equally distributed over all hives. Hives were, in fact, clumped in few apiaries in each study area. The mean number of foragers removed per hive per day over three months varied from 53 in the first sampling (M1) to 116 in the last one (L2), being on average 73. Thus, the daily predation over recruitment, *i.e.* the proportion of mortality due to bee-eaters over the total daily mortality (or recruitment) of workers in each hive (3 % of the total bee population in a hive, *i.e.* in our case 1,200 workers a day), represented on average 6.1 % (range: 4.4-9.7 %) of the daily worker mortality in a hive.

The mean number of drones removed per hive per day over three months ranged from 1.1 (M1) to 5.8 (L2) being on average 3.4. Assuming a daily recruitment/mortality of 12 drones, *i.e.* the 1 % of worker daily recruitment or 3 %

of the drone population in the hive, bee-eater daily predation represented in mean 30.5 % of the daily drones recruitment/mortality in a hive (range 9.1-48.3 %). These figures were quite dramatic because in some areas, *e.g.* Corongiu, drone mortality due to bee-eaters may have outnumbered their daily recruitment (22 drones preyed on per day per hive in June, *i.e.* 183 % of the daily recruitment) leading to a rapid decline of the local drone population. Thus, the most serious losses of drones may have occurred in localities with low bee availability, where surprisingly no complaints from bee-keepers were recorded.

DISCUSSION

Reliability of results

Reliable calculation of predation impact required three sets of data, each being a possible source of bias: numbers of bee-eaters, numbers of honey bees, and rates of prey consumption by birds. Numbers of bee-eaters could have been underestimated because nests that failed early were not counted although adults could be still around. Breeding failure may occur due to bad weather (and hence shortage of prey) or predation, but in general a full replacement-clutch can be laid, even in a new burrow providing that the season is not too advanced (Tapfer, 1957; Fry, 1984). In our Mediterranean study areas the main cause of breeding failure is predation by fox (*Vulpes vulpes*). However, proportions of nests preyed on by fox in our bee-eater colonies ranged from less than 1 % to 5 % of total nests (pers. observ.). Thus, numbers of failed breeders around colonies should have been very low. Nevertheless, we assumed that 20 % of nests were attended for by a bird trio (two parents and a helper) and this figure may largely compensate for uncounted adults that failed to breed.

The numbers of bees available to bee-eaters we assumed (40,000 workers and then 20,000 foragers per hive) may be, if any, an underestimate since in Italy most hives contain as much as 80,000 workers (and then 40,000 foragers; Dietz, 1982; R. Cirone and other bee-keepers, pers. comm.; P. Galeotti and M. Inglisa, pers. observ.) and an average of 30,000 foraging bees per hive might be a more realistic figure. Nonetheless, we took into account the lowest of these availability estimates, in order to consider the worst damage hypothesis. The working assumption of a constant hive population size through the study period could have been an approximation, however, because of seasonal variations in number of worker bees and drones. In particular, bee population is known to increase during the flower season, which results, if the hive is not man-managed, in a growing prey availability from May to July. If this was the case, the actual bee availability in the study areas would have been greater and predation impact consequently lower than our estimates.

Possible bias in predation estimates can also originate from pellet analyses. For example, our model made no allowance for bees that were killed or damaged but did not show up in the bird pellet. However we think this is a negligible fraction because, firstly, the mean predation rate we found (25.2 prey per pellet) gave a daily consumption of 126 prey per bird, a value well whithin the range and very near to the maximum consumption rate derived from literature (56-150 prey per bird per day, Biber, 1971; Ursprung, 1979; Fry, 1984; Martinez, 1984; Inglisa

et al., 1993). Secondly, predation rate on bees (8 bees/pellet, range 0-47) was higher than the mean value (5 bees/pellet) derived from literature (Biber, 1971; Ursprung, 1979; Martinez, 1984; B. Massa, pers. comm.). Thirdly, from our data a bee-eater consumed 40 bees per day (39 workers and one drone per day), thus assuming a biomass of 6.8 g, that was nearly 18 % of its daily food requirement (39 g, Fry, 1984). The other 86 prey consumed daily by a bee-eater on the basis of our calculations may well be enough to meet the remaining 32 g of its daily food requirements. Therefore, we generally believe that our estimates of bee-eater predation on honeybees and other insects are correct.

BEE-EATER PREDATION ON BEES AND DRONES

This study shows that bee-eaters preyed on foraging bees largely in relation to their mean availability over all areas through the sampling period. Thus, bees constituted the bulk of bee-eater diets where they were the majority of flying insects, but were a marginal prey-item where they were rare (Riola).

Functional response by bee-eaters in Sardinia (measured by pellet content with an assumption of constant number of pellet per day) was linear, at least in the interval of prey availability we examined (type I functional response, according to Holling, 1959). In other words, bee-eater predation on foraging bees was not diluted at higher prey-density, as by contrast occurs in a functional response of type II (Holling, 1959). Consequently the predation impact by bee-eaters was constant over most range of bee densities (0.27 % in May-June) and increased in relation to bee-eater rather than to prey density. In July, when number of consumers practically triplicated (adult bee-eaters foraged also for chicks), predation impact doubled (0.56 %). Actually, bee-keepers seem to complain of damage to their apiaries only where bee-eater colonies are numerous and conspicuous, while no complaints about bee-eater predation come from areas with small bee-eater populations.

However, from our results, the mortality caused by bee-eaters was on average no more than 6 % of the daily worker recruitment in each hive (*i.e.,* 73 foraging bees removed per day per hive), so that losses of foragers were in fact negligible at all densities of bees we examined, and even less if bee-density was higher than estimated.

Losses of drones due to bee-eaters may be more important and might account for the virtual extinction of the local drone population in areas with low bee-availability. Although drones are produced in excess in the hive and one male is enough to fertilize millions of eggs of a queen, the rarity of males due to high predation pressure may reduce mating opportunity eventually leading to a loss in genetic diversity (bottleneck). This might be a problem for both the amateur and specialized bee-keepers (*i.e.,* queen's breeders). However, as we have shown, predation impact on drones is inversely density-dependent, so that drone predation is diluted at high bee-densities. Also, the extinction of drones in July may not be influential on reproduction because the bulk of mating occurs in spring (April to June); finally most professional bee-keepers and many amateurs are now using the insertion of already fertilized queens or the artificial fertilization. Taken together, these findings suggest that bee-eaters predation on drones, although disproportionate, cannot seriously damage hive life and honey production in areas with high bee-availability, but might locally create some problems to small or specialized apicultures.

In conclusion, we can rule out that bee-eaters cause economically relevant damage to intensive apiculture and shooting of birds is definitely not justified because their impact is generally very low. Refunds of losses, if any, may be admitted for amateur and specialized bee-keepers.

MANAGEMENT IMPLICATIONS

In order to minimize or eliminate losses to apiaries we may suggest, at first, that apiaries should not be installed within 5-10 km of bee-eater colonies or potential colony sites. This measure alone would prevent much damage, especially to nomadic apiaries. Avoiding bird areas may be unrealistic however, since bee-keepers locate their hives where bees can take the best advantage of the available nectar and pollen availability.

Secondly, increasing bee-density until the optimum level compatible with food supply and avoiding interference competition may greatly reduce predation impact on drones, whitout increasing predation impact on foragers.

Finally, bee-eaters feed at apiaries mainly during bad weather at the beginning and end of season when parent birds are not "tied" to the nest site (K. Lessels, pers. comm. and pers. observ.). Shutting the hives during such conditions (when bees do not in any case forage efficiently) and at those times would be very effective at virtually eliminating bee predation by bee-eaters.

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REFERENCES

BIBER, O. (1971). — Contribution à la biologie de reproduction et à l'alimentation du Guêpier d'Europe *Merops apiaster* en Camargue. *Alauda*, 39: 209-212.

BODENHEIMER, F.S. (1958). — *Animal ecology today*. Monogr. Biol. 6. Dr W. Junk, Den Haag, Netherlands.

BRIAN, M.V. (1965). — *Social Insect Populations*. Academic Press, London.

BUYS, B. (1975). — A survey of honeybee pests in South Africa. Pp. 185-189, *in:* H.J. Durr, H.J. Gilliomeee & S. Neser (Eds). *Proceedings 1 Congress Entomological Society of South Africa*.

CANO, A. (1960). — Sobre nidificación communal y alimentación del Abejaruco (*Merops apiaster*). *Ardeola*, 6: 324-326.

CAVANI, C. (1991). — The quality of the diet of foxes (*Vulpes vulpes*) in a Mediterranean coastal area (central Italy). *Histrix*, 3: 63.

DIETZ, A. (1982). — Honey Bees. Pp. 323-369, *in:* H.R. Hermann (Ed.). *Social Insects*, Vol. III. Academic Press, London.

FRY, C.H. (1983). — Honeybee predation by bee-eaters, with economic considerations. *Bee World*, 64: 65-78.

FRY, C.H. (1984). — *The Bee-eaters*. T & A D Poyser Ltd, Calton.

GRENCI, S., MASSA, B., NOBILE, V. & RIZZO, M.C. (1997). — Importanza degli Imenotteri (Insecta Hymenoptera) nella dieta del Gruccione *Merops apiaster* L. (Aves Meropidae). *Naturalista siciliano*, 21: 287-307.

GROUT, R.A. (1981). — *L'Ape e l'Arnia.* Edagricole, Bologna.

HELBIG, A. (1982). — Zur Nahrungsökologie eines norddeutschen Bienenfresser (*Merops apiaster*). Paares mit Überlegungen zum Aufreten in nördlichen Mitteleuropa. *Die Vogelwelt*, 103: 161-175.

HOLLING, C.S. (1959). — The component of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, 91: 293-320.

INGLISA, M., GALEOTTI, P. & VIGNA-TAGLIANTI, A. (1993). — The diet of a coastal population of European bee-eaters (*Merops apiaster*) compared to prey availability (Tuscany, central Italy). *Boll. Zool.*, 60: 307-310.

JENN, R.A.Y. (1973). — Ravages of the bee-eater. *American Bee Journal*, 113: 21.

KOENIG, L. (1969). — Der Nahrungsverbrauchjunger *Melittophagus bullockoides* (Meropidae) während der Entwicklungszeit. *Österr. Akad. Wiss. Math.-Naturwiss.*, 178: 323-336.

KORELOV, M.N. (1948). — [Information on the ecology and economic significance of Golden Bee-eaters] (in Russian). *Izvestia Academy Nauk Kazakhstan SSRepublic, Zoology service*, 51: 107-123.

KORODI GAL, J. & LIBUS, A. (1968). — Beiträge zur Kenntnis der Brutnahrung des Bienenfressers (*Merops apiaster* L.). *Zool. Abh. Berl. Mus. Tierk.*, 29: 95-102.

KREBS, J.R. & AVERY, M.I. (1985). — Central place foraging in the European bee-eater, *Merops apiaster. J. Anim. Ecol.*, 54: 459-472.

LESSELS, C.M. & AVERY, M.I. (1989). — Hatching asynchrony in European Bee-eaters *Merops apiaster. J. Anim. Ecol.*, 58: 815-835.

MARTINEZ, C. (1984). — Notes sur l'alimentation du Guêpier (*Merops apiaster*) dans une colonie du centre de l'Espagne. *Alauda*, 52: 45-50.

MATOUSEK, B. (1951). - [Biology of the Bee-eater in Slovakia.] (In Czech with English summary). *Sylvia*, 13: 122-125.

PETROV, V.S. (1954). — [Concerning the feeding ecology of Golden Bee-eaters]. (In Russian). *Works of Scientific Investigation of the Institute of Biology & Biology Faculty, Kharkov University (Ukraine)*, 20: 171-180.

RUTTNER, F. (1966). — The life and flight activity of drones. *Bees World*, 47: 93-100.

SZEDERKÉNYI, N., FAUST, R., VARGA, G., TÁRNOKY, E., DÉKÁNY, D. & KOLTAY, P. (1956). — [Damage to bees by bee-eaters] (in Hungarian). *Méhészet*, 3: 125-126.

SWIFT, J.J. (1959). — Le Guêpier d'Europe *Merops apiaster* L. en Camargue. *Alauda*, 27: 97-143.

TAPFER, D. (1957). — Über die Verbreitung und Brutbiologie des Bienenfressers in Ungarn. *Falke*, 4: 3-5.

TOSTAIN, O. (1978). — Nidification du Guêpier d'Europe *Merops apiaster* et observations de la Cisticole des joncs *Cisticola juncidis* en Seine-et-Marne. *L'Oiseau Rev. Fr. Orn.*, 48: 184.

URSPRUNG, J. (1979). — Zur Ernahrungbiologie ostösterreichischer Bienenfresser (*Merops apiaster*). *Egretta*, 22: 4-17.

VIGNA TAGLIANTI, A., INGLISA, M. & MEI, M. (1988). — Metodologie per l'analisi dell'alimentazione di una specie entomofaga. *Naturalista siciliano*, 12: 105-108.

WOLDHEK, S. (1979). — Bird killing in the Mediterranean. *European Committee for prevention of Mass Destruction of Migratory Birds.* Zeist, Netherlands.

YAKUBANIS, V.N. & LITVAK, M.D. (1962). — [Feeding of the Golden Bee-eater in the Dniester area, Moldavia] (in Russian). Pp. 49-55, in: *Collected Essays on problems in ecology of practical significance regarding birds of Moldavia.*